More than taking the heat: crops and global change

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Grain production per unit of land will need to more than double over this century to address rising population and demand. This at a time when the procedures that have delivered increased yields over the past 50 years may have reached their ceiling for some of the world's most important crops. Rising global temperature and more frequent droughts will act to drive down yields. The projected rise in atmospheric $[CO_2]$ by mid-century could in theory increase crop photosynthesis by over 30%, but this is not realized in grain yields in current C_3 cultivars in the field. Emerging understanding of gene networks controlling responses to these environmental changes indicates biotechnological opportunities for adaptation. Considerably more basic research, particularly under realistic field conditions, is critical before these opportunities can be adequately understood and validated. Given the time needed between discovery in a model plant species and translation to traits or stacked changes in a commercial grain crop cultivar, there is an urgent need to vigorously pursue and develop these opportunities now.

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An impending grain drain?

Nothing is more important to humanity and the stability of societies, than a reliable and affordable supply of food. Climate change will clearly alter where crops can be grown and their productivity, the extent to which this will affect global food supply remains controversial. The Intergovernmental Panel on Climate Change (IPCC) concluded that despite climate change and increasing world population, crop surpluses at the global level would continue resulting in a 'small decline in real world food (cereals) prices' over this century [1]. IPCC predicted that only if global mean temperature rises by more than 5.5°C will global food prices increase because of failure of supply to keep full pace with demand. IPCC assumed yield improvements of 80% by 2050, continuing the trend of the second half of the 20th century. Can we expect the year-on-year increases of the last half of the 20th century to continue? China is the world's largest producer of rice, the world's most important food in terms of the number of people dependent on it as a direct source of calories. Between 1987 and 1997 its average production (t/ha) rose 17%, but only 2% between 1997 and 2007 [2], despite continued genetic improvement. At the global scale, wheat, the second most important caloric source for humans, rose 20% in production from 1987 to 1997, but global yield declined 1% from 1997 to 2007 (Figure 1). Of the world's three most important grains, only maize maintained the rate of increase of the 1970s and 1980s into the most recent decade [2] (Figure 1). In contrast to IPCC projections, these facts suggest that capacity for continued increase is approaching a ceiling. Increase in yield potential over the past 50 years has resulted by increasing partitioning of biomass into grain (harvest index; HI) and increasing the proportion of available sunlight energy that the crop intercepts during the growing season [3]. Today's best germplasm partitions over 60% of total biomass into grain and intercepts over 90% of growing season radiation by the crop leaf canopy, suggesting little room for further improvement here [3]. Improved photosynthetic and respiratory efficiency, remain the only theoretical major routes for further substantial improvements in genetic yield potential. These traits have proved far less tractable to conventional breeding than HI [3]. So while the ceiling might be raised, it will require considerably more effort while simultaneously adapting to climate change.

Is climate change affecting our ability to continue increasing yield? Australia, historically among the four largest wheat exporters, has in the last seven years suffered unprecedented droughts and its wheat yields averaged 25% less than the previous seven [2]. Changes in our ability to produce grain are also occurring against important global economic changes that are increasing consumption. In 1990, net imports of dry soybeans to China were 1.1 Mt, but 32.8 Mt by 2007, a rise from 1% of total global production to 15%, and this despite increased domestic production [2]. In summary, and assuming little further capacity to expand agricultural land area, grain production per unit land area will need to more than double over this century to deal with rising population and dietary change. We examine how three key global change factors rising temperature, declining water availability, and rising atmospheric $[CO_2]$ will

Figure 1
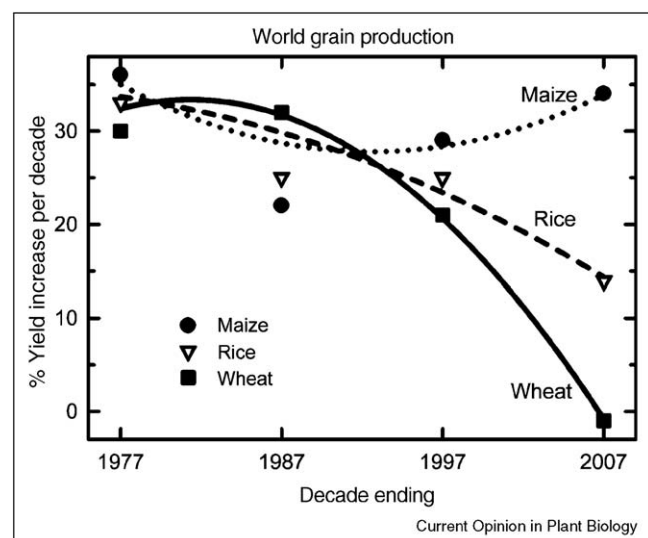
Increase (%) in world production per decade of the three major cereal grains, based on UN Food and Agriculture Organization records [2]; with 2007 as the last year for which complete data were available. Global production of grain in 2007 was maize 788 Mt, paddy rice 657 Mt and wheat 611 Mt compared to 272, 277 and 294 Mt, respectively in 1967. Wheat and rice gains have declined over the past two decades, only maize has continued to maintain the increases of earlier decades; calculated from [2].

affect grain production and knowledge gaps, as well as strategies for preventing these changes from becoming a grain drain; Table 1 summarizes these effects.

Taking the heat

The accumulation of greenhouse gases in the atmosphere is driving a warming trend that is projected to continue throughout this century. Decreases in agricultural yield are already linked to increases in growing season temperatures [4]. For example, an increase of 1.5–2°C is projected for the US during the next 50 years and 3–6°C by the end of the century [5]. Increase in average temperature could result in longer potential growing seasons at high latitudes, and often shorter seasons at low latitudes because of interactions with rainfall, evapotranspiration and soil moisture. The optimum climates for our major grains will move poleward, such that the N. American wheat and corn belts will move northwards into Canada, with parallel changes on the Eurasian steppe [1]. However, this does not mean that yields can be maintained simply by moving the production areas poleward. These areas lack the high quality soils of the prairie and steppe. At other locations, for example the wheat belt of western Australia, poleward movement is not possible since the ocean lies to the south. Perhaps of greater importance, than the general warming trend, is the prediction of an increase in the frequency of heat-waves [6].

Table 1

Summary of expected effects of atmospheric and climatic change on yields of our major grain crops, outlining caveats including possible interactions between temperature, water and atmospheric composition

Atmospheric variable	Yield	Caveats
Increased temperature (high latitudes[a])	↑↑	↓Optimal climate zones will move onto suboptimal soils ↓Daylength will complicate adaptation to higher latitudes ↑Rising CO_2 may amplify effect of increased temperature in C_3 crops
Increased temperature (low latitudes)	↓↓↓	↓↓Exacerbate drought by increasing evapotranspiration ↓↓Increased probability of lethal high temperature events ↓Will increase probability of damaging ozone events ↑Rising CO_2 will offset increased photorespiration
Drought (high latitudes)	↓	↑Decreased incidence of water logging, allowing earlier harvesting and less interference with farm operations ↑Rising CO_2 will lower evapotranspiration ↓Increased probability of crop failure ↓↓Pollination and grainset could be impaired
Drought (low latitudes)	↓↓↓	↑Rising CO_2 will lower evapotranspiration ↓↓Increased probability of crop failure ↓↓↓Pollination and grainset could be impaired ↓Exacerbates risk of leaves reaching lethal high temperatures
Rising [CO_2]	↑↑↑	↓Observed effect under open field conditions lower than anticipated and little or absent in C_4 crops ↑Partial protection against drought ↑Partial protection against ozone ↑Benefit in decreasing C_3 crop photorespiratory losses, increases with temperature ↓Decreased leaf latent heat loss will increase probability of attaining lethal high temperatures
Overall	??	There have been almost no field scale studies of how temperature, drought and rising CO_2 interact in affecting our major grains. Predictions are based largely on chamber studies which bear almost no resemblance to farmers fields, or on year-to-year variation in climate which fail to include the unprecedented projected future changes in atmospheric composition. As a result, all predictions of future global grain supply have to be viewed as highly tentative

[a] High latitudes, ca. >50° and low latitudes ca. <45°.

The response of photosynthesis to higher temperature will be a major driver of temperature effects on yield. The primary carboxylation reaction of photosynthesis catalyzed by Rubisco (Ribulose 1:5 bisphosphate carboxylase/oxygenase) is directly affected by temperature [7••]. Whereas the rate of carboxylation by Rubisco increases with temperature up to or even beyond 50°C, increased solubility of O_2 relative to CO_2 and decreased discrimination against oxygenation by Rubisco increase photorespiratory CO_2 loss as a proportion of photosynthetic uptake. The rate of RubP regeneration can be even more sensitive to temperature than RubP carboxylation and is much more variable with growth conditions and among species [8]. In both C_3 and C_4 plants, mitochondrial respiration increases with short-term increases in temperature, causing a commensurate decrease in net photosynthesis, although long-term responses are less clear. Moderate increases in temperature, just above the optimum, have other damaging effects on photosynthesis. Rubisco activase, the chloroplast protein that regulates the portion of Rubisco that is catalytically active, is highly sensitive to moderate heat stress while catalytic misfires, which inactivate Rubisco also increase with temperature and inhibit Rubisco limited photosynthesis at temperatures as low as 36°C [9,10••]. Thylakoid membrane conductance to ions becomes compromised in cotton leaves with moderate temperature increases affecting the transmembrane proton-motive force needed for ATP formation, and in turn the RubP-limited rate of CO_2 uptake [11]. Increased temperature is associated with other factors which lower CO_2 assimilation by decreasing stomatal conductance. In particular, evaporative demand increases with temperature, even if relative humidity remains constant, causing stomata to close and in turn reduce transpiration and photosynthesis, while increasing leaf temperature further because of decreased latent heat loss.

What can be done to improve the tolerance of photosynthesis to rising temperatures? Gene shuffling has been used to improve the thermal stability of Rubisco activase in *Arabidopsis* resulting in increased rates of photosynthesis and production under moderate heat stress [12•]. Lowering photorespiratory flux will reduce the inhibition of C_3 photosynthesis by rising temperature. Engineering foreign algal Rubisco's with higher specificity could in part address this problem [3]. Although higher specificity is usually at the expense of k_{cat}, this would be partially compensated by increased catalytic rate at higher temperature [13]. More promising is a photorespiratory bypass engineered in *Arabidopsis* chloroplasts by the introduction of the *E. coli* glycolate catabolic pathway that substantially decreases the energetic cost of increased photorespiration [14]. This in turn would be expected to increase the temperature optimum of net photosynthesis in these transformed plants. Additionally, the overexpression of SbPase, which has been shown to

stimulate RubP-limited photosynthesis and productivity [15], protects against the inhibition of photosynthesis by moderate heat stress [16]. Rubisco activase might also be protected by increasing the expression of the associated chloroplast GroEL homolog (cpn60β), which, given its homology to other hsp60s, could be expected to protect against heat stress [10••].

Although crop yield is frequently limited in the field by carbon gain, the optimum temperature for photosynthesis, vegetative growth, and reproductive development is nearly always higher than the seasonal temperature optimum for yield. Thus, while any inhibition of photosynthesis caused by high temperature excursions in the future should be expected to result in reduced yield, the temperature dependence of other physiological processes will play a critical role. Higher temperatures commonly decrease the time to flowering and life cycle in grain crops, so decreasing the period over which photosynthesis can occur. Ability to regulate the gene networks that control these responses could prevent this undesirable crop response [17••]. In addition, because high temperatures affect pollen viability and fertilization, a heat stress event during pollination can severely reduce yield even when the seasonal average is within a favorable range. Overall, yield is highly sensitive to temperature, such that even the ~0.7°C of anthropogenic warming to date has caused yield loss [18•,19,20].

Drying out

Water availability dominates global crop yields [21]. The water holding capacity of air, or in effect its drying power, increases exponentially with temperature. Therefore, even with no change in precipitation, increased evapotranspiration driven by higher air temperature will increase drought incidence. An analysis of the northeastern U.S. predicts increased growing season soil water deficits even with little or no change in annual precipitation [22]. The IPCC projected that the land area affected by drought will increase and water resources in affected areas could decline as much as 30% by mid-century [5]. Improving the yield of crops grown under drought conditions has been difficult because of the low heritability of tolerance, varied effects depending on timing of drought, and gaps in understanding of drought physiology [23–25]. However, recent genomic approaches have identified a suite of genes that regulate drought adaptation or otherwise confer drought tolerance that, when coupled with transgenic technologies, have resulted in rapid progress in improving drought tolerance. This shows considerable promise for production agriculture [17••].

Two inter-connected but distinct characters should be distinguished in considering drought tolerance: Firstly, ability to survive the low water potential of a drought, which include the traits of increased concentrations of

osmotica to avoid cellular dehydration, minimization of water loss by stomatal closure and stay green to maintain the crop canopy. Essentially these traits enhance ability to 'sit out' a drought until water is again available. Secondly, water use efficiency (WUE) is the amount of dry mass that the plant produces for a given quantity of transpired water. High WUE will of course also increase the ability of a plant to survive drought, simply by conserving soil water reserves. WUE is primarily determined by the physics of diffusion, that is the concentration gradients of CO_2 and water vapor between the atmosphere and leaf intercellular space, and the conductances for the two gases along this diffusion pathway. It is therefore less variable and tractable to selection than the traits directly affecting drought tolerance. In general it appears easier to increase the ability of crops to tolerate drought as opposed to increasing ability to use water more efficiently. C_4 plants do have intrinsically higher WUE, because they maintain a lower intercellular $[CO_2]$ and therefore greater diffusion gradient. Typically this is about 75% higher for a given atmospheric water vapor pressure deficit. Decreasing the intercellular $[CO_2]$ in C_3 leaves by engineering a photorespiratory bypass [14] or a plasmalemma bicarbonate pump [26•], as in some algae, could potentially achieve similar WUE improvements in C_3 plants.

Although intrinsic WUE differs little within photosynthetic types, consistent small differences have been identified. Quantitative trait loci for water use efficiency have been identified in numerous species, but only recently have the actual genes contributing improved WUE been identified. ERECTA, which codes for a leucine-rich repeat receptor kinase, was shown to be involved in regulating WUE [27]. Improved WUE is of limited or perhaps even negative benefit where ample water is available throughout most or all of cropping cycle but confers benefit in drier environments that depend on stored soil moisture from winter precipitation as the main source of growing season moisture [28]. In principle, improving intrinsic WUE by increased photosynthesis (e.g. by increased mesophyll conductance) rather than decreased transpiration would confer a growth and yield benefit even when water is plentiful but there is little evidence for this response by plants.

Engaging multiple stress pathways by manipulating the expression of specific transcription factors (TFs) has proved to have significant promise in improving drought tolerance. The CBF/DREB TFs act to modulate a set of genes that define a major stress tolerance pathway. Coupling drought-responsive promoters to target CBF/DREB overexpression to coincide with water deficit has provided proof of concept for improved engineered drought tolerance [29,30]. Directed expression of the maize CAAT box TF confers marked drought tolerance that translates into increased yield of transgenic maize under field conditions [31•]. These are but two of

numerous emerging examples (e.g. [32–34]) in which the overexpression of selected classes of TFs have been observed to improve drought tolerance. Another transgenic approach for which there is field validation of improved growth and yield with drought under field conditions is the introduction of bacterial RNA chaperones into maize and rice [35••]. A functional RNA binding site is required for these proteins to confer drought tolerance, implying that these proteins act directly on transcripts perhaps to rescue mRNAs that become misfolded during a stress episode. Improved drought tolerance using transgenic technologies to overexpress or time the expression of TFs, as well as other proteins that regulate drought adaptation, is projected to be among the next major introduced traits that will be released commercially [36•].

Carbonating the atmosphere

Rising atmospheric $[CO_2]$ is the largest single driver of global warming, but as a limiting substrate for photosynthesis it also directly increases plant production. Before the Industrial Revolution, the concentration was about $270 \ \mu mol \ mol^{-1}$. It has risen at an ever increasing rate since then, reaching $387 \ \mu mol \ mol^{-1}$ in 2009 and projected to increase to $550 \ \mu mol \ mol^{-1}$ by mid-century and possibly $800 \ \mu mol \ mol^{-1}$ by 2100. The one positive of global change for food production has appeared to be rising atmospheric CO_2. The direct increase in C_3 photosynthesis on elevation of $[CO_2]$ results from two properties of Rubisco. Firstly, the K_m of the enzyme for CO_2 is close to the current atmospheric concentration, so elevated $[CO_2]$ increases the velocity of carboxylation. Secondly, CO_2 competitively inhibits the oxygenation reaction, which produces glycolate and in turn photorespiratory release of CO_2. On the basis of the average and largely conserved kinetic properties of Rubisco for C_3 crops, and a constant intercellular versus external $[CO_2]$, increase in atmospheric $[CO_2]$ to $550 \ \mu mol \ mol^{-1}$ would increase RubP-saturated photosynthesis by 34% at 25°C, with even greater improvements at higher temperatures [37]. In C_4 plants no direct response is expected because PEP carboxylase, which catalyze the primary carboxylation of C_4 photosynthesis, is 'CO_2' saturated at today's atmospheric $[CO_2]$. Therefore, only when the CO_2 supply is strongly restricted because of decreased stomatal conductance can a direct response of photosynthesis to increasing $[CO_2]$ occur in C_4 plants. In both C_3 and C_4 plants, stomatal conductance declines in inverse proportion to $[CO_2]$ causing decreased evapotranspiration and increased leaf temperature [38]. This decrease in evapotranspiration improves WUE which could indirectly increase yield in both C_3 and C_4 plants during drought. Elevation of $[CO_2]$ to $550 \ \mu mol \ mol^{-1}$ in controlled environments and small field chambers results in yield increases in C_3 grain crops of about 30%, and up to 15% in C_4 grains. However, in the large open-air Free Air Concentration Enrichment (FACE) facilities (Figure 2),

Figure 2

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A view of 1 of 16 Free Air Concentration Enrichment (FACE) octagonal plots at the SoyFACE facility in central Illinois. CO_2 is released by the octagon of horizontal pipes according to wind direction and speed to maintain a constant elevation of $[CO_2]$ within the 350-m^2 plot. This facility has examined the season-long effect of elevated $[CO_2]$ on soybean and maize [37,38].

which provide the most realistic approximation of the future currently available, yield increases are only half that seen in chamber experiments, while C_4 grains show little or no response [39] (Figure 3).

Figure 3
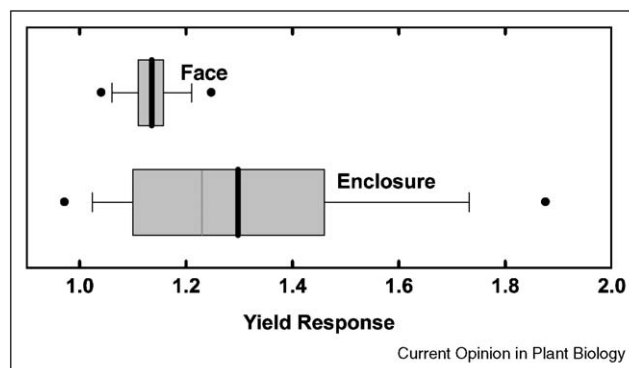
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Box plot of the yield response ratios from free-air CO_2 enrichment (FACE) and chamber experiments. The thick black line shows the mean, and error bars represent 10th and 90th percentiles. The FACE data have an average ambient $[CO_2]$ of 367 μmol mol^{-1} and an elevated $[CO_2]$ of 583 μmol mol^{-1} with a mean yield response ratio of 14%. The chambers have an average ambient $[CO_2]$ of 373 μmol mol^{-1} and elevated $[CO_2]$ of 565 μmol mol^{-1} with a mean yield response ratio of 31%. The higher chamber value is statistically significant ($P = 0.016$; Wilcoxon–Mann–Whitney two-sample test). Reproduced with permission from [39].

Why might realized yield increases under field conditions fall short of expectation? The genomes of these crops undoubtedly carry much of the adaptation that occurred before domestication, where selection was not for yield, but for survival. While under modern agronomy nutrients and in many situations water are provided, in the wild there would be strong selection against an individual outgrowing its resources. Yield response to elevated $[CO_2]$ declines strongly with soil resistance to root penetration [40], which may act as a measure of the resource available for the completion of the life cycle. Roots likely signal such factors through TFs and hormone interactions at the root tip [41]. Analysis of genetic changes that have led to the greater yields of our major grain crops, relative to their wild ancestors, show significant changes in regulatory networks controlled by TFs. Now that these are increasingly understood, substantial further gains in yield are anticipated through alteration of their regulation [17**]. Early flowering is likely another conservative trait that ensures completion of the life cycle and survival in the wild at the cost of yield. Disruption of the GIGANTEA gene of *Arabidopsis*, delayed flowering and produced a much larger phenotype [42]. If these and similar changes do represent modifications that make the plant less conservative, and so raise the productivity ceiling, then it follows that these forms will be more capable of realizing the full potential increase in photosynthetic productivity under elevated $[CO_2]$.

Rubisco in higher plants has a remarkably low catalytic rate (k_{cat}). Although the exact basis for the low k_{cat} is unknown, one of the most plausible explanations is that this is a penalty for the high specificity (τ) for CO_2 relative to O_2. This is necessary to minimize oxygenation and the subsequent loss of carbon in photorespiration. Support for this hypothesis is given by the fact that organisms adapted to high CO_2 or/and low O_2 environments have forms of Rubisco with a higher k_{cat} and lower τ [43]. Theoretical analysis suggests that the form of Rubisco in modern C_3 crops is optimal for the average [CO_2] of the past 25 M years (ca. 220 μmol mol^{-1}). Engineering foreign Rubisco's with a k_{cat}/τ optimal to today's [CO_2] could increase carbon assimilation by 10%, for the same total quantity of Rubisco [43]. Even without change in the form of Rubisco, rising [CO_2] increases the rate of carboxylation and increasingly shifts metabolic control of photosynthetic rate away from Rubisco to regeneration of the CO_2 acceptor molecule, RubP. Regeneration of RubP is controlled potentially by more than 60 proteins. Analysis of a complete dynamic metabolic model of C_3 photosynthetic carbon metabolism, suggested that for the same total investment in protein a 60% increase in photosynthetic rate could be achieved by re-optimizing resource investment for 550 μmol mol^{-1} [CO_2]. In particular, the study suggested increased investment in chloroplastic sedoheptulose-1:7 bisphosphatase (SbPase) and downstream enzymes involved in storage carbohydrate synthesis, at the expense of enzymes of photorespiratory metabolism [44]. Transgenic overexpression of SbPase has already been shown to increase photosynthesis and the yield of tobacco [45•], it will now be critical to establish if this yield enhancement is amplified at elevated [CO_2] as anticipated from theory. So far we have considered targeted changes to enhance crop responses to rising [CO_2], most associated with photosynthesis. There is considerable evidence of genetic variability within crop germplasm in yield response to elevated [CO_2] [46]. Association mapping would provide an important first step in revealing further genetics underlying variation in response, and in turn other traits that could realize the theoretical 30% yield increase at 550 μmol mol^{-1} [CO_2], as opposed to the realized 14% in current germplasm. Such mapping however would require the provision of large-scale field enrichment facilities to test the 200+ lines required for such an analysis [47].

Conclusion
While debate continues around whether climate change will cause global grain shortages or not, on the precautionary principle the world needs to be prepared. The cost of undertaking the basic research and precommercial development to achieve adaptations to rising temperature, drought incidence and [CO_2] will be small compared to the social and economic disruptions, not to mention the human cost, of serious grain shortages. While we have outlined some targets above, these are only scraping the

surface of the regulatory networks that will need to be modified to achieve adaptation. Rapidly evolving tools may allow these to be unraveled in *Arabidopsis* and other model organisms. 2050 may sound a long way away and a chance for several more years of discussion. However, given the time required to translate findings in model organisms to crops, complete the long regulatory process for releasing new transgenics, and then bulk seeds for commercial release, even starting now might only be just in time.

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